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Patterns in the distribution
of the
Southern African amphibia

The ranges of the various forms of amphibians in southern Africa conform to a few very distinctive basic patterns. The distribution of the southern African Amphibia has already been outlined in a general way (Poynton, 1960), and the aim of this paper is to show selected examples of the different types of patterns. It is not proposed to give here a close analysis of the factors which might be responsible for imposing common patterns on different amphibian forms. The profound differences in the ecology of different amphibians in southern Africa should, however, be emphasized in order to discourage any simple explanation of the determination of amphibian distribution patterns. For example, species of *Xenopus* Wagler are almost totally aquatic, whereas species of *Breviceps* Merrem and *Arthroleptis* Smith pass the entire life cycle away from water. The fact that animals of such diverse ecology as the Amphibia conform to the same general patterning indicates that one must look for causal factors beyond features such as water and soil composition, and even vegetation, to the fundamental background of the prevailing temperature and rainfall. The complexity of the situation is further shown by there being not one but six different basic patterns shown by the Amphibia in southern Africa. Examples of each type of pattern are here presented with the intention of inviting comparisons from workers on the distribution of other groups, since the more general these patterns turn out to be, the easier should be the task of explaining them.

The Tropical Pattern. No tropical form covers the whole of southern Africa. The ranges of two of the most widespread tropical forms, *Phrynobatrachus natalensis* (Smith) and *Kassina senegalensis* (Duméril and Bibron), are shown in Figs. 1 and 2 respectively. Neither of these occur in the south-western Cape, a feature common to all tropical forms. These forms are also absent from the arid south-west region of Bechuanaland and most of the Great Karoo, and as a result their distribution patterns take on a characteristic trifurcated shape, radiating out from the tropical north-east. Only seven of the forty tropical forms occur in South West Africa, and the distribution of less widespread forms is illustrated by *Chiromantis xerampelina* Peters and *Bufo carens* Smith (Figs. 3 and 4). Such forms show a characteristic bifurcated pattern, one arm extending down the east coast and another up the Limpopo basin towards Griqualand West. It is notable that of the twenty tropical forms that pass south of the Tugela River in Natal, ten also extend inland to the Mafeking area in this way. Forms showing this bifurcated pattern appear to be governed largely by summer conditions, since summer temperatures in the Mafeking area and the east coast are similar, while the Mafeking area

is much colder in winter. The bifurcated pattern is brought about by these forms tending to avoid the highveld, which is cooler both in summer and winter. This pattern cannot be correlated with the rainfall pattern, although clearly the western margin is determined mainly by the aridity of the Kalahari.

Other tropical forms, including the great majority of the treefrog family (Rhacophoridae), are further restricted in that they do not extend far up the Limpopo basin, although they extend some distance down the eastern coastal lowlands of South Africa (e.g. *Hyperolius pusillus* (Cope), Fig. 5). Approximately one-third of the tropical forms are confined to the area experiencing a tropical climate in Koppen's sense (Poynton, 1960). *Xenopus muelleri* Peters provides an example of a tropical distribution pattern (Fig. 6). All the other tropical forms considered above are ones which contribute to the subtraction margin of the tropical fauna, which lies outside the tropical region.

An extraordinary pattern is shown by two tropical species of *Pyxicephalus* Tschudi. Both species are very widespread, but neither occurs in the Natal and Pondoland lowlands. The bullfrog (*P. adspersus* Tschudi) displays this pattern well (Fig. 7). The cause of this anomaly is completely obscure.

The Transitional Patterns. The Natal and Pondoland lowlands carry eight endemic forms, the majority of which are closely related to tropical forms. *Arthroleptis wahlbergi* Smith is a typical example (Fig. 8). Eastern Southern Rhodesia is a similar subtropical centre of endemism (e.g. *A. venodaetlyoides* Hewitt, Fig. 8), and this area shares some non-tropical forms with the South African eastern plateau slopes.

Another transitional group is centred in the Natal highlands and the south-eastern Cape lowlands, e.g. *Breviceps adspersus pentheri* Werner, Fig. 9. This subspecies occurs above the 4,000 ft. contour in Natal, the tropical nominate form occurring below this level. The 13° C mean midwinter isotherm runs along this contour in Natal, and it marks a zone where the fauna changes from being predominantly tropical to being predominantly temperate. Fig. 10 gives an interesting example of a tropical form (*Afrizalus b. brachyememis* (Boulenger)) which has apparently given rise to a tropical transitional form (*A. spinifrons* (Cope)) on the lowlands, and a temperate transitional form (*A. knysnae* (Loveridge)) in the Natal highlands and the south-eastern Cape.

The Natal Drakensberg shows a relatively high incidence of very localized endemics, there being four forms confined to this escarpment. The Amatola Mountains have two endemic forms, and there is one endemic on the Transvaal Drakensberg (Woodbush). Such very localized endemics are unusual amongst the Amphibia. Seven eastern transitional forms cover most of Natal and the eastern Cape, and also a part of the Transvaal, e.g. *Pyxicephalus natalensis* Smith (Fig. 11) and *Rana f. fasciata* auct. (Fig. 12). *R. fasciata* also has a relict population on the Southern Rhodesian highlands.

Of the western transitional forms, one group extends from Angola and Northern Rhodesia to the border area of southern Africa, or beyond into South West Africa and or Southern Rhodesia (e.g. *Xenopus laevis poweri* Hewitt, Fig. 13). Another group of seven forms occurs on portions of the western plateau slopes (e.g. *Cacosternum namaquense* Werner, Fig. 14).

The Temperate Pattern. Two representatives of the Cape fauna cover all of southern Africa except the Mozambique plain, the central Kalahari and the Namib desert (e.g. *Xenopus l. laevis* (Daudin), Fig. 15. *Rana grayi* Smith is more restricted (Fig. 16) but it has left relict populations in eastern Rhodesia and the arid west. *Kassina wealii* Boulenger leaves the Cape only on the moist eastern highlands (Fig. 17). Six temperate forms in this way pass beyond the area of the proposed Cape region (Poynton, 1960), the area of this region being occupied by, among others, *Hyperolius horstoki* (Tschudi) (Fig. 18). Two-thirds of the Cape forms, however, have restricted ranges within the Cape region, the majority being confined to an area within a hundred-mile radius of Cape Town.

It is notable that typical relict distribution patterns are shown by temperate and transitional forms, but not by any tropical forms. This situation is a clear indication that Southern Africa as a whole has recently been warming up. Amphibian distribution does not necessarily indicate a significant increase in aridity as well, although this is suggested by the distribution pattern of *Rana grayi* in the west.

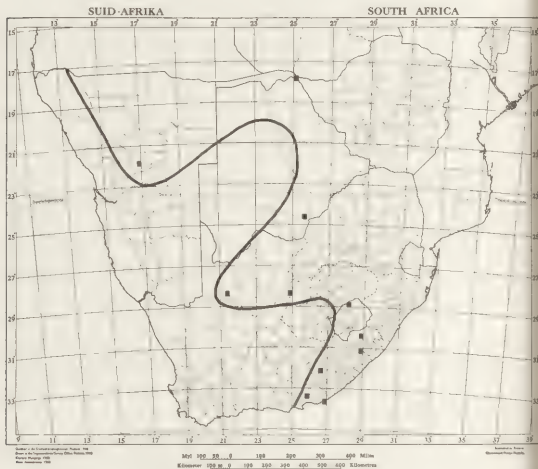


Fig. 1. *Phrynobatrachus natalensis* (Smith). Only marginal localities shown.

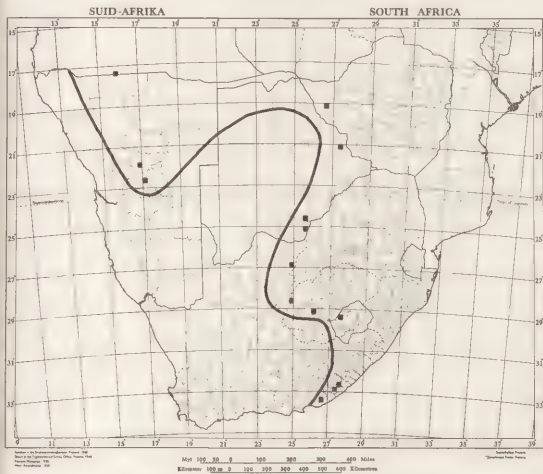


Fig. 2. *Kassina senegalensis* (D. & B.). Only marginal localities shown.

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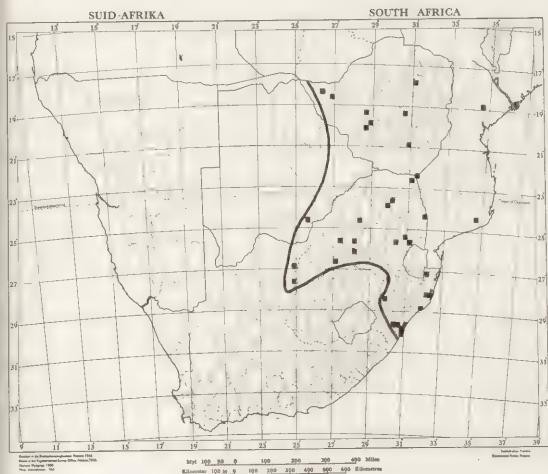
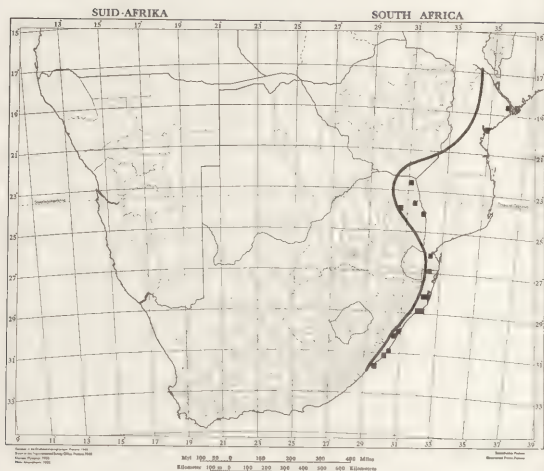


Fig. 4. *Bufo carens* Smith.

Fig. 5. *Hyperolius pusillus* (Cope).

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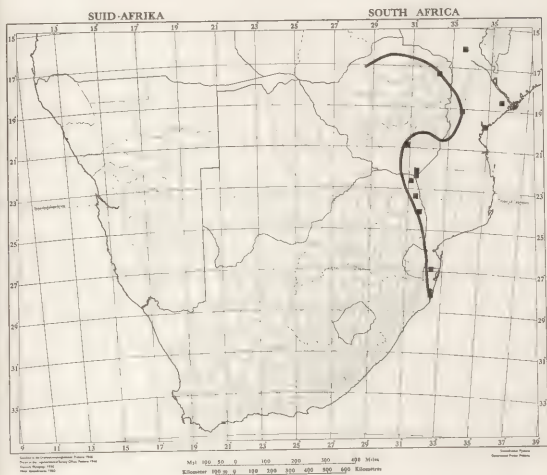
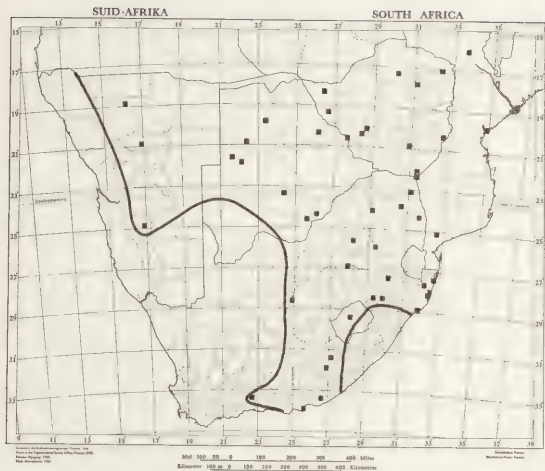


Fig. 6. *Xenopus muelleri* Peters.

Fig. 7. *Pyxicephalus adspersus* Tschudi.

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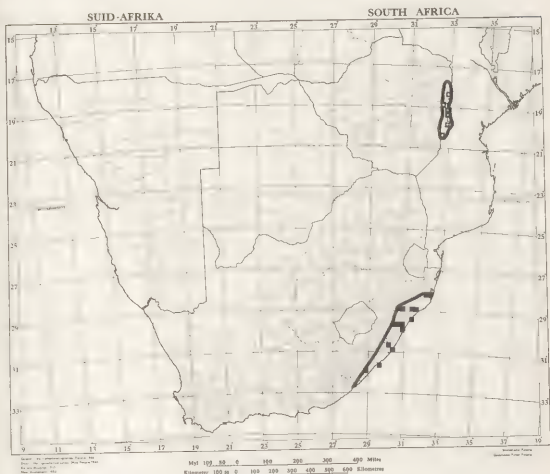
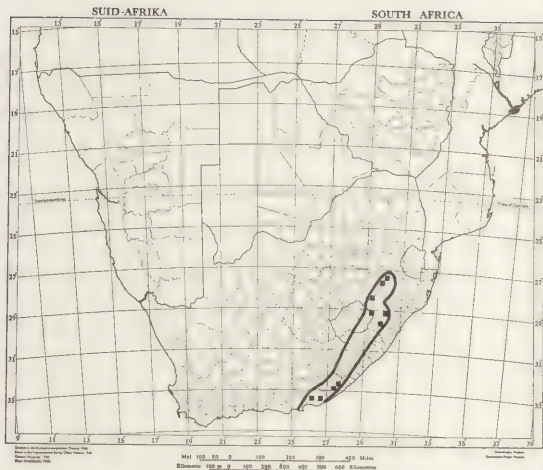


Fig. 8. ■ *Arthroleptis wahlbergi* Smith.
□ *Arthroleptis xenodactyloides* Hewitt.

Fig. 9. *Breviceps pentheri* Werner.

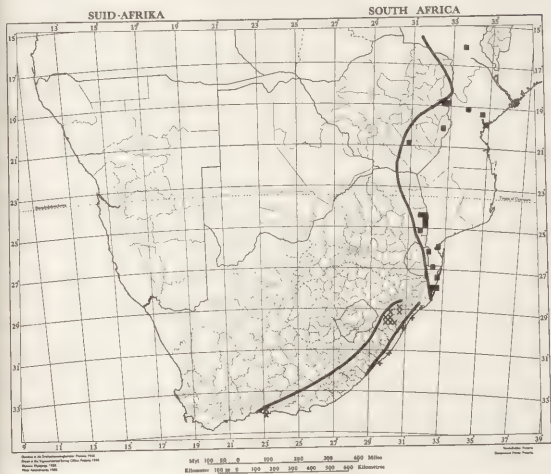
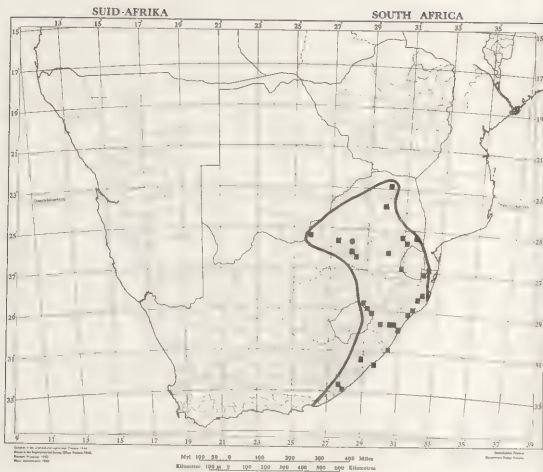


Fig. 10. ■ *Afrixalus b. brachycnemis* (Boulenger).
+ *Afrixalus spinifrons* (Cope).
× *Afrixalus knysnae* (Loveridge).

Fig. 11. *Pyxicephalus natalensis* Smith.

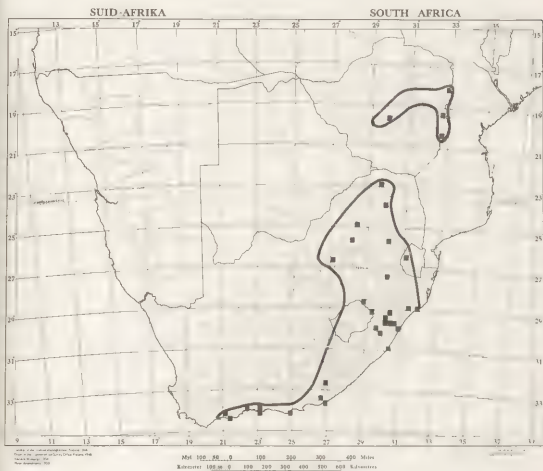
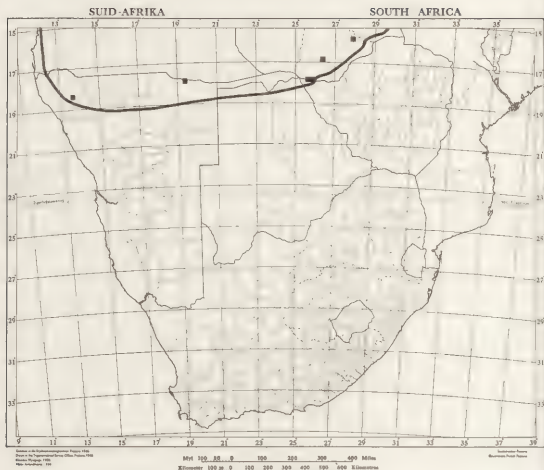


Fig. 12. *Rana fasciata auct.*

Fig. 13. *Xenopus laevis poweri* Hewitt.

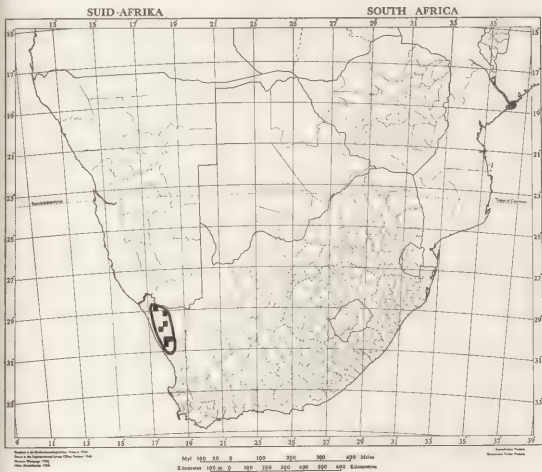


Fig. 14. *Cacosternum namaquense* Werner.

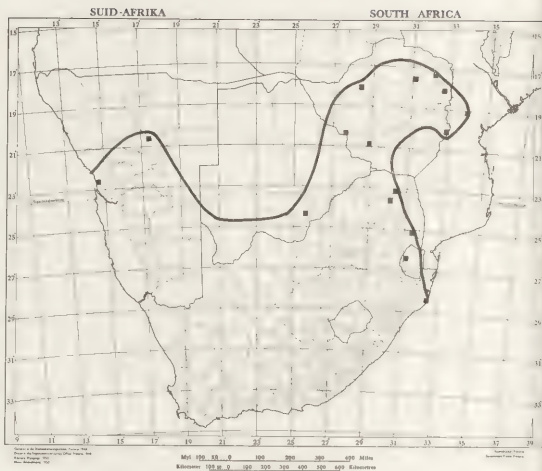


Fig. 15. *Xenopus l. laevis* (Daudin). Only marginal localities shown.

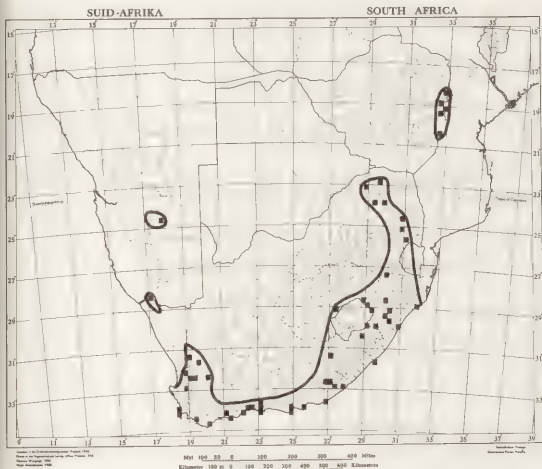
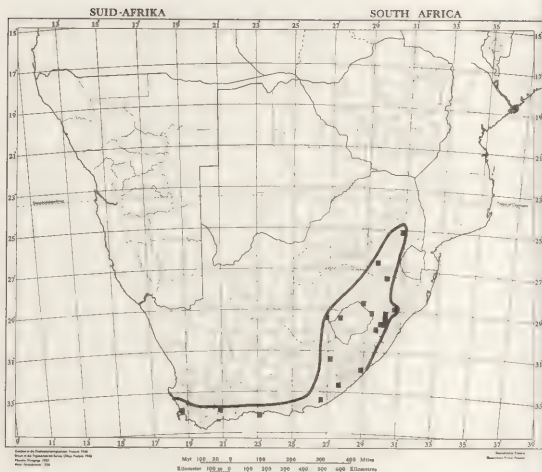


Fig. 16. *Rana grayi* Smith.

Fig. 17. *Kassina wealii* Boulenger.

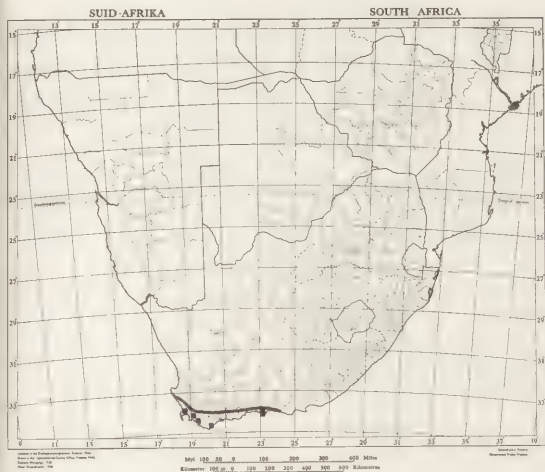


Fig. 18. *Hyperolius horstoki* (Tschudi).

REFERENCE

- POYNTON, J. C. 1960. Preliminary Note on the Zoogeography of the Amphibia in Southern Africa, *S.A.J. Sci.*, 56: 307-12.

DISCUSSION

- Prof. Ewer:* I understand that the 4,000 ft. contour in Natal, which coincides with the 13° C mean midwinter isotherm, also marks the line above which wattles can be grown and below which they cannot. (Dr. Poynton confirms and adds that trout also do not come below this line.) The point I wish to make is that these animals are amphibian and thus likely to be affected by the fact that the highlands tend to be particularly wet and misty and also by the fact that the character of the waters, especially running waters, differs above and below 4,000 ft. Many frogs are extraordinarily fussy in regard to the type of water in which they will oviposit. In mentioning these matters, I am seeking an alternative to the postulated correlation with temperature. I think the controlling factor might be something else. I do not believe that animals are as sensitive as thermometers; and I think that putting animal distribution on a map and looking for other matching things, also on maps, tends to be misleading and to obscure other correlations.
- Dr. Poynton:* I agree that to say that distribution matches temperature is not to answer the problems. However, I can find no correlation with moisture at the 4,000 ft. level, nor with any other factor that might affect amphibian distribution. Further, several of our frogs are not strictly tied to water, but even species of such genera as *Breviceps* and *Arthroleptis* tell the same story. Thus, whether or not the eggs are laid in water the same pattern emerges.